Estimated Population Size and Home Range of the Salamanders Plethodon jordani and Plethodon glutinosus

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ABSTRACT

In a study area in the Great Smoky Mountains National Park, North Carolina, the density of *Plethodon jordani* (one individual for every 12.5 ft^2) was estimated to be about 4 times that of *Plethodon glutinosus* (1 individual for every 46.3 ft^2). The proportion recaptured estimates agreed well with the Lincoln-index estimates. Male *P. jordani* moved significantly farther between captures than female or juvenile *P. jordani*. For *P. jordani*, the estimated home range sizes were: males, 123.5 ft^2; females, 30.3 ft^2; juveniles, 18.5 ft^2. For *P. glutinosus*, the estimated home range sizes were: males, 154.9 ft^2; females, 70.2 ft^2; juveniles, 81.1 ft^2. Within the study area, both species were associated with large logs and trees. The adults of the 2 species did not appear to be intermixed within the study area.

Regardless of the parameter being considered, the impact of a species upon the community in which it lives is dependent upon the density of that species. In this respect, the density of a species becomes an important constant by which the influence of the individual member of the species must be multiplied in order to determine the quantitative effect of the species upon its environment.

Plethodon jordani Blatchley and *Plethodon glutinosus* (Green) are 2 closely related species of lungless woodland salamanders which are sympatric in some areas of the southern Appalachian Mountains (Hairston, 1951; Highton, 1962). In these areas, it is readily apparent to collectors that the 2 forms are not equally abundant. Closer study of the relative abundance in a given area might better quantify the numerical relationships of these 2 species.

With these considerations in mind, a study, the objective of which was the estimation of the relative densities of these forms in an area where they were sympatric, was undertaken during the summers of 1963, 1964, and 1965. Mark-release techniques were employed so that the movements of individual salamanders could be monitored throughout the summer. This provided information regarding the home range, migration, and dispersion, as well as density of the 2 species.

The study area was located 50 yards north of a small creek (Taywa Creek) at an elevation of 4,000 ft. above sea level on the western slope of Hughes Ridge in the Great Smoky Mountains National Park, Swain County, North Carolina. A grid 100 x 50 ft. was established such that the long axis extended in an east-west direction. Population size estimates were made for the eastern half of the study area (Fig. 1). For the first 2 summers, the entire 5,000 ft^2 were used in the study of movements and home range. Throughout the grid, stakes were placed at

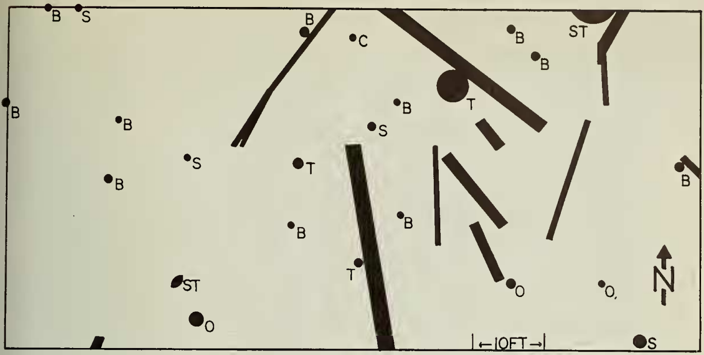

Fig. 1. Scale diagram of the study area. The population size estimates reported in the text are for the eastern half of the study area. The entire area was used to study movements and home range during 1963 and 1964. Darkened rectangular areas represent fallen logs greater than 4 inches in diameter. Other objects are stumps (St) or trees greater than 4 inches in diameter: beech (B), silverbell (S), tulip (T), oak (O), cherry (C).

intervals of 10 ft., subdividing the grid into 50 ten-by-ten squares, and making no point in the grid more than 7 ft from a stake. Of the 12 trees greater than 4 inches dbh, 5 were beech (*Fagus grandifolia*), 2 were silverbell-tree (*Halesia carolina*), 2 were red oak (*Quercus rubra*), 2 were tulip-tree (*Liriodendron tulipifera*), and 1 was cherry (*Prunus* sp.). Of the 12 trees that were less than 4 inches dbh (but were at least 5 ft tall before the trunk forked), 11 were beech (*Fagus grandifolia*), and 1 was sugar maple (*Acer saccharum*). The floor was covered with much litter and debris including decaying chestnut (*Castanea dentata*).

Materials and Methods

As an attempt to standardize the level of darkness at which sampling began, entering the grid was delayed until it became too dark to see a given tree from a fixed place 10 yards away. As soon as this level of darkness was reached, a systematic search of the study area along established routes was begun. In order to avoid sampling the same portion of the grid at the same time, the place of initial sampling was determined randomly.

While sampling, the grid was carefully scrutinized with the aid of a 6-v dry cell-powered lantern. Only animals found walking on the surface or extending part-way from burrows were recorded. Thus there was a minimum of destruction to the habitat. When an animal was observed, it was captured and identified as to species and sex. If it had not previously been marked, a unique combination of toes was clipped with scissors or fingernail clippers. The animal was measured (tip of snout to anterior angle of vent) in millimeters by stretching it along the edge of a ruler. The distance from the nearest stake was estimated. The animal was then released exactly where it had been captured, taking care to see that when released, at least the animal's head was beneath a leaf or similar object so that the light and further activity in the immediate vicinity would not disturb it. This precaution was taken after it was observed that occasionally a released animal would start moving rapidly away and in a straight line—neither of which it had been doing before it was captured. Animals thus carefully released were never observed to begin moving rapidly, but would either push their way farther under the leaves or would remain stationary with their heads under the leaves. Normally, depending upon the number of animals present on the surface, from 2 to 4 hr were spent in this manner going through the grid. Identification as to sex was based upon the fact that the adult males of these species possess a swollen mental gland beneath the chin. Animals without the gland and greater than 44 mm (snout-vent length) were considered to be adult females. Without the gland and less than 48 mm, they were regarded as juveniles. Because of regeneration of the toes, marking could not be recognized from one summer to the next, and so new marking were given to all animals each year. Sampling in 1963 extended from June 14 through September 1; in 1964, from June 16 through July 19; in 1965, from June 13 through August 24.

In arriving at an estimate of the population size, the data gathered in the above manner were analyzed in 2 ways. In the first analysis, use was made of the Lincoln-index technique in which P = MN/m (where P is the estimate of the population size, M is the number of marked animals released into the population, N is the size of a subsequent sample, and m is the number of marked animals in the subsequent sample). Since more than 2 samples were taken, the same method was applied by grouping the samples into 2 groups—a marking and a recapture group. Outings were grouped such that the 1st half of the samples were considered as used for marking and releasing, and the 2nd half of the samples were considered as used for recapturing. In all cases, for an odd number of samples, the odd sample was included in the marking and releasing group.

The standard deviations associated with the Lincoln-index estimates were calculated using the method summarized by Southwood (1966), in which the variance associated with the estimate is given by the following formula:

$$\text{Var P} = \frac{M^2N(N-m)}{m^3}$$

where: M, N, and m are as defined above.

The second method of analyzing the data made use of the fact that as marked animals were continually released into the population, subsequent samples showed an increase in the proportion of marked animals. This increase in proportion of marked animals should continue until at 1 point, subsequent samples consist of 100% marked animals (Hayne, 1949b). In the present study, the point of 100% recaptures was never reached, but the population size was estimated by fitting the best line (method of least squares) to a plot of proportion recaptured vs. the cumulative marked. From the resulting graph, the number of animals needed to be marked to give 100% recaptures was determined. The fitted line as pointed out by Hayne (1949b) must be forced through the origin, since at 0 cumulative marked, 0 recaptures is the only possible observation.

The size of the home range of an individual was estimated by using the method described by Hayne (1949a). In this method, the center of activity of an individual animal was determined by calculating the geometric center of the capture locations. The average distance from this center of activity to the capture locations was calculated and was used as the radius of the home range. The estimated home range then extended as a circle around the center of activity.

Results

The results obtained by using the Lincoln-index methods of estimating numbers are reported in Table 1 for *Plethodon jordani* and in Table 2 for *Plethodon glutinosus*.

The proportion recaptured results for *P. jordani* are presented graphically in Fig. 2 and are summarized in Table 3. The data for *P. glutinosus* were not treated with this method because the sample sizes were too small.

Support for the hypothesis that the population of *P. jordani* did not change from year to year was obtained by comparison of the rate at which the population was marked each year. If the population were greatly larger or smaller one year than another, then the rate at which the population was marked should be significantly different. The slope of the lines in Fig. 2 is a measure of the rate at which the population was marked. Confidence intervals for the slopes were calculated according to Snedecor and Cochran (1967). The 95% confidence intervals for the slopes all overlapped, and so there was no significant difference in the rate at which the population was marked from one year to the

Table 1. Estimated number of *Plethodon jordani* using the Lincoln-index method. See text for method of calculating the standard error.

Number of Samples in Estimate	1963	1964	1965
2	39 ± 25.4	—	196 ± 188.9
3	170 ± 161.3	95 ± 60.1	102 ± 104.6
4	102 ± 53.8	171 ± 114.0	144 ± 74.9
5	140 ± 56.7	—	148 ± 90.6
6	140 ± 44.6	208 ± 112.8	159 ± 52.5
7	188 ± 99.1	198 ± 73.5	153 ± 38.1
8	162 ± 40.4	193 ± 61.6	163 ± 37.8
9	162 ± 31.1	156 ± 41.5	177 ± 36.2
10	166 ± 31.2	156 ± 34.9	198 ± 41.4
11	165 ± 26.8	219 ± 53.4	203 ± 34.7
12	167 ± 26.0		198 ± 31.9
13	186 ± 27.5		202 ± 29.4
14	187 ± 27.3		217 ± 31.7
15	221 ± 34.7		217 ± 28.4
16	230 ± 35.1		228 ± 27.7
17	244 ± 35.6		
18	243 ± 34.3		
19	243 ± 32.2		
20	249 ± 33.0		
21	268 ± 37.2		
22	278 ± 38.5		
23	289 ± 40.0		
24	283 ± 37.2		
25	277 ± 31.9		
26	283 ± 31.7		
27	275 ± 29.7		
28	295 ± 32.4		
29	248 ± 22.0		
30	295 ± 27.0		
31	295 ± 21.0		
Ave. est. number: 216 174 184			
Ave. est. number for all 3 years: 200			

next. Since the differences among the years were not significant at the 95% level, a combined regression line was fitted to all the data, and a combined estimate calculated (Fig. 2 and Table 3). Using the confidence limits of the slopes, estimated population sizes were calculated, and the resulting range of values are reported in Table 3.

The points of capture for each individual were mapped and the distances moved between captures were measured. The resulting distribution of movements approximated a Poisson distribution, so the data were transformed by using the transformation $(x + 1)^{1/2}$ (Snedecor and Cochran, 1967). The transformed data were then subjected to an analysis of variance (Table 4). The mean male, female, and juvenile movements and the mean for each year are reported in Fig. 3. In view of the non-overlapping of the confidence interval of the males with that of the females or juveniles, it was decided that separate estimates of the male, female, and juvenile home range size should be made. The lack of a significant difference between the years indicated that the average movement was not significantly different from year to year, and so all movements within a sex were summed over the 3 years to obtain the results in Tables 5 and 6. Because of the small number of individuals involved, and because of the large variation observed in the results obtained, no statistical analysis of the movements or home range size of *P. glutinosus* was performed. The results reported for *P. glutinosus* are therefore estimates, the validity of which is unmeasured.

The results of estimating the home ranges are in Table 5 for *P. jordani* and in Table 6 for *P. glutinosus*. Individuals which were

Table 2. Estimated number of *Plethodon glutinosus* using the Lincoln-index method. See text for method of calculating the standard error.

Number of Samples in Estimate	1963	1964	1965
2	—	—	—
3	—	—	—
4	—	—	—
5	—	—	—
6	—	12 ± 6.9	—
7	35 ± 19.2	14 ± 8.4	—
8	63 ± 39.3	20 ± 10.0	—
9	51 ± 35.3	20 ± 20.0	—
10	61 ± 30.7	37 ± 11.9	—
11	48 ± 17.5	52 ± 33.8	—
12	51 ± 19.0		—
13	54 ± 20.2		—
14	58 ± 21.7		50 ± 14.1
15	45 ± 12.4		50 ± 14.1
16	45 ± 12.4		37 ± 9.7
17	44 ± 11.8		
18	53 ± 15.5		
19	55 ± 15.6		
20	55 ± 15.6		
21	68 ± 23.7		
22	78 ± 28.5		
23	101 ± 43.4		
24	73 ± 22.0		
25	77 ± 21.7		
26	71 ± 18.6		
27	60 ± 12.0		
28	60 ± 11.6		
29	62 ± 12.1		
30	62 ± 12.5		
31	64 ± 12.7		
Ave. est. number: 60 26 46			
Ave. est. number for all 3 years: 53			

captured only 2 times are included in the results in Tables 5 and 6. Their inclusion in Table 5, however, does not alter the conclusions, since the large variance associated with the estimates calculated on the basis of 3 or more captures included the mean calculated on the basis of only 2 captures. Again, the small sample size of *P. glutinosus* prevented such a comparison for that species.

In obtaining the results in Tables 5 and 6, the home ranges are represented as circles. It must be emphasized that no claim is made to the effect that the actual home ranges are circular. The circles are merely a convenient estimate of the size of the home range.

It was readily apparent while in the field that not all portions of the study grid were used to the same degree by the salamanders. Thus, an analysis of the dispersion of the individuals within the study area became a consideration. The total number of captures within each 10-ft subsquare was determined, and a variance/mean ratio for the resulting data was calcualted. For *P. jordani*, this ratio equalled 8.964, and for *P. glutinosus*, the ratio was 5.059. Both ratios were significantly greater than expected on the basis of chance (*P. jordani*: $t = 29.822$, $df = 49$, $P < .001$; *P. glutinosus*: $t = 20.296$, $df = 49$, $P < .001$). A variance/mean ratio significantly greater than one indicates a clumped dispersion (Greig-Smith, 1964). Comparison of the centers of activity with the distribution of large objects (logs and trees) in the study area (Fig. 1) suggested that the dispersion might be associated with the distribution of the large objects. The area occupied by large logs and trees plus an area bounded by 1 ft in all directions from the edges of these objects represented 26% of the total area in the

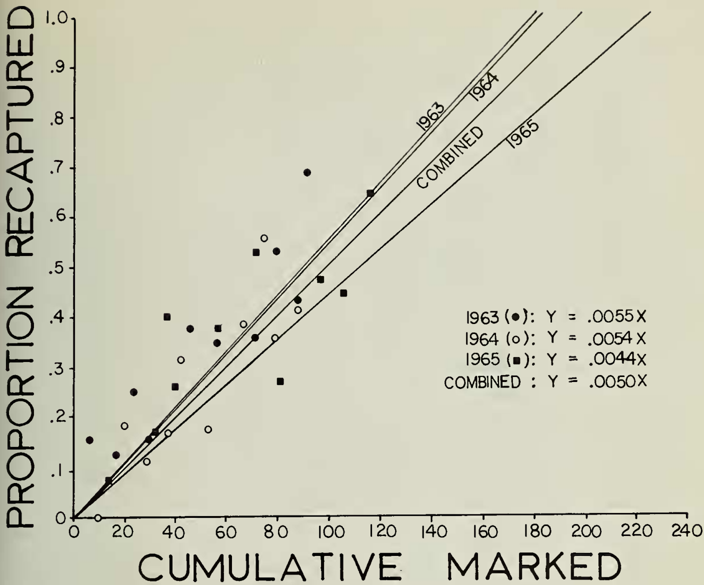

Fig. 2. Proportion recaptured vs. cumulative marked. Thepopulation size estimates (i.e. the values on the abscissa corresponding to the point 1.0 on the ordinate) for 1963, 1964, 1965, and for all years combined are respectively 182, 185, 227, and 200 individuals. See Table 3 for the confidence intervals of the slopes.

study area. The distance of 1 ft from the edge of these objects was arbitrarily decided to be a reasonable quantitative estimate of "close to" these objects. If the animals were distributed about the area independently of the objects within it, then there should be proportionally no greater number of captures "close to" the objects than "far from" them. Comparison of the observed number of captures "close to" and "far from" the large objects for each year with the number expected on the basis of the proportion of the total area which the objects occupy revealed that there was a significantly greater number of captures "close to" the large objects that expected on the basis of the area occupied by the objects (*P. jordani*: $X^2 = 18.96$, df - 1, $P < .005$; *P. glutinosus*: $X^2 = 10.45$, df = 1, $P < .005$).

The number of centers of activity falling "close to" large objects and the number of centers of activity falling "far from" large objects for each year was not significantly different from what was expected on the basis of the number of captures occurring "close to" and "far from" large objects (*P. jordani*: $X^2 = 0.29$, df = 2, $.75 < P < .90$; *P. glutinosus*: $X^2 = 3.74$, df = 2, $.10 < P < .25$).

If one ignores juveniles, then *P. jordani* and *P. glutinosus* had centers of activity which did not appear to be readily interspersed but rather appeared to be grouped in different regions of the study area.

Discussion

It is concluded that the density of *Plethodon jordani* in the study area was about

Table 3. Population size estimates of *Plethodon jordani* based on the proportion recaptured method.

Year	Slope	Est. population size	95% confidence interval of slope	Range of Population-size estimates based on confidence interval of slope
1963	.0055	182	$.0072 > b > .0038$	139-263
1964	.0054	185	$.0065 > b > .0025$	154-400
1965	.0044	227	$.0063 > b > .0025$	159-400
Combined	.0050	200	$.0060 > b > .0040$	167-250

200 animals per 2500 ft^2, or 1 *P. jordani* for every 12.5 ft^2. *Plethodon glutinosus* was found to be only about ¼ as abundant as *P. jordani*, there being an estimated 54 *P. glutinosus* in the study area, or 1 *P. glutinosus* for every 46 ft^2.

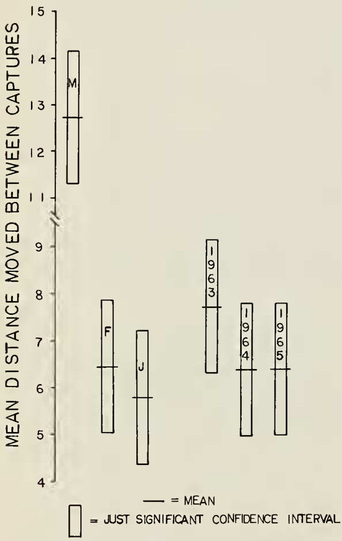

Fig. 3. Comparison of mean movements in feet between captures for *Plethodon jordani*. The means for males, females, and juveniles summed over years are compared and the means for 1963, 1964, and 1965 summed over sex are compared. Non-overlapping Just Significant Confidence Intervals (JSCI's) indicate significant differences at the 95% level. JSCI corresponds to the D value of Snedecor and Cochran (1967).

While other estimates of the population density of *P. jordani* and *P. glutinosus* are not available for comparison with the results obtained in the present study, several estimates of the population density of *Plethodon cinereus* have been reported. Burger (1935), working in Pennsylvania and New Jersey, stated that densities of *P. cinereus* may equal 1 individual for every 18 ft^2. Test and Bingham (1948) reported densities in Michigan of 1 individual for every 189 ft^2, but implied that the real density was greater. Klein (1960) in Pennsylvania estimated the density of *P. cinereus* to be 1 individual for every 51 ft^2.

The present study was an attempt to estimate the number of salamanders in the open on the surface and during the time period of approximately 8:30 to 11:30 P.M.. The major assumption was that on successive nights the same population was being dealt with. Taub (1961) found that with mark-release techniques applied to caged populations of *P. cinereus*, better estimates (estimates closer to the actual number present) were obtained when the individuals were kept on the litter and not permitted to penetrate to lower soil layers. Thus exchange of individuals between the lower soil levels and the litter layer—which could not be prevented in the field study—have undoubtedly influenced the estimates herein reported. Horizontal migration, while not conclusively disproved, is assumed to be of little importance in the present study for several reasons. First, whenever studies have been made of *Plethodon* with regard to horizontal movements of non-displaced individuals, no evidence for their occurrence has been uncovered. Klein (1960) reported that no marked *P. cinereus* were found outside his study area; Test and Bingham (1948) stated that there appeared

Table 4. Analysis of variance for movements of *Plethodon jordani*.

Source	DF	SS	MS	EMS
Total	455	1551.2433		
Years	2	25.9660	12.9830	$\sigma^2 + \sigma_s^2 + 2.2\sigma_i^2 + 51.7\sigma_s^2 + 130.3\sigma_y^2$
Sex (years)	6	260.7156	43.4526	$\sigma^2 + \sigma_s^2 + 1.8\sigma_i^2 + 46.6\sigma_s^2$
Individ. (sex)	245	886.8456	3.6198	$\sigma^2 + \sigma_s^2 + 1.8\sigma_i^2$
Samples (individ.)	202	377.7131	1.8699	$\sigma^2 + \sigma_s^2$

to be little shifting in the population after a census had been taken. Taub (1961) reported no evidence of horizontal migration of *P. cinereus*. Highton (1956) reported that the largest observed movement between captures of marked *P. glutinosus* was 14.5 ft. This movement took place during an interval of 28 days, however, other individuals showed no movement over intervals of as much as 341 days. Secondly, searches of the peripheral area in the present study and the direction of recorded movements within the study area gave no indication of migration. Thirdly, a significant difference in the percentage of animals recaptured in inner areas of the grid (44.75%) vs. the percentage of animals recaptured in border areas of the grid (45.89%) might have indicated migration, but no such difference was found. Comparison of the number of recaptured individuals and the number of individuals never recaptured in border and inner squares gave a X^2 value of 0.12 (df = 1, $.50 < P < .75$).

Variation within an individual's activity period (as measured by its being out in the open) may also have contributed to the error in the estimates. On several occasions, the study area was sampled a second time, beginning after the 1st sample was completed at approximately 11:30 P.M.. When 2 samples were taken on the same night, the majority of the animals in the 2nd sample were different from those taken in the earlier sample. The 2nd sample always included animals which had been marked in 8:30-11:30 samples. A more striking aspect of this can be seen by looking at the results of a sample taken from 3:00-4:00 A.M. in another study area. In this sample, all the animals which were recaptured had been marked in 8:30-11:30 samples. The percentage of recaptures (50%) in this early morning sample was greater than the percentage (27%) in the sample taken at 11:30 P.M. the night before. In addition, 1 marked animal captured at 3:00 A.M. was recaptured again at 8:30 P.M. that night. Thus it appears that a given animal does not always have the same period of activity. This report includes only data taken in 8:30-11:30 samples, and thus differences in activity periods of an individual as well as vertical migration could have influenced the estimated numbers reported herein.

The movement-between-captures data for *P. jordani* were highly variable, and no attempt was made to eliminate outliers. In spite of this, the difference in the mean movement between males and females or juveniles was significant, and thus the difference can be taken as a biologically real and presumbably important difference associated with the sex of the individual. A possible explanation of this difference may be related to the reproductive behavior of this species. The general pattern of courtship of the plethodontid salamanders has been described by Noble and Brady (1930), and that of *P. jordani* and *P. glutinsosus* by Organ (1958, 1960). In these descriptions, it is the male that initiates courtship, the role of the female during the initial phases being described as passive. Thus, the larger home range of the males may be the result of their moving farther during periods of activity which results, during the breeding season, in a greater probability of their contacting a receptive female.

The fact that there was no significant difference between the mean home range of *P. jordani* based upon 3 or more captures, and the mean home range based upon 2 captures is expected, considering that the small number of captures for a given individual probably does not indicate loss of the individual from the study area but probably means that the individual was either not at the surface or was not active at the time of

Table 5. Estimated mean radius and mean area of home range of *Plethodon jordani.*

Year	Radius of home range in ft			Area of home range in ft^2		
	Males	Females	Juveniles	Males	Females	Juveniles
1963	6.43	3.56	2.35	128.68	39.81	17.35
1964	6.73[a]	2.75	2.52	141.02[a]	23.76	19.95
1965	5.38	2.46	2.51	91.61	19.01	19.79
Ave.	6.27	3.11	2.42	123.46	30.27	18.46

[a]Based on less than 10 animals.

Table 6. Estimated mean radius and mean area of home range of *Plethodon glutinosus.*

Year	Radius of home range in ft			Area of home range in ft^2		
	Males	Females	Juveniles	Males	Females	Juveniles
1963	7.70[a]	3.06[a]	5.88[a]	186.26[a]	29.42[a]	108.66[a]
1964	9.20[b]	8.63	—	256.99[b]	233.86	—
1965	1.50[b]	—	3.65[a]	7.07[b]	—	41.85[a]
Ave.	7.02[a]	4.73	5.08	154.88[a]	70.24	81.11

[a]Based on less than 10 animals.

[b]based on 1 animal.

the survey. In addition, in many cases the 2 captures were 4 or more weeks apart, thereby supporting the hypothesis that only 2 captures does not necessarily indicate a home range which is really an artifact of the method of analysis applied to an individual which does not actually have a home range.

The selection of 1 ft away from the edge of large objects as a measure of "close to" the objects, while arbitrary, was not unreasonable since it is well within the mean distance moved between captures of both sexes and juveniles.

The agreement between the location of the centers of activity and the locations of capture indicates that the mathematically determined centers of activity reflect the biology of the species in 2 ways. First, the centers of activity are positionally located "close to" large objects in the area as are the sites of capture. Thus, an individual animal directs its activities about these objects. Secondly, the individual's movements, as revealed by changes in the location of capture, are such that for the most part they do not cross large areas that lack either large logs or large trees. If such areas were crossed, then, although the individual might always be captured near large objects, the geometric center of the capture sites would more often that was observed by shifted away from the objects toward the center of the areas lacking large objects.

The interesting aspect of the association of *P. jordani* and *P. glutinosus* with large logs or trees is that the asosciation exists after dark. Daytime collection of these forms reveals that, in general, more individuals are found by looking beside or under logs, bark, stones, etc. than by scratching around under leaves. But the daytime association is not just the result of retreat into sheltered areas which the individuals abandon after dark. The activity of the animal after dark, as revealed by its position at the time of capture, is also restricted to areas "close to" these large objects. The association with large objects is not necessarily to the exclusion of smaller objects, and in fact, the association with large trees may very well be due to the fact that many of the trees possessed hollow bases, sloughed off bark around the base, or obvious crevices about the visible portion of the roots. There probably are minimum requirements which cover must fulfill before it is suitable—requirements that a layer of fallen leaves does not fulfill—and which are provided by objects other than large logs and large trees, but the data as collected do not include the location of these smaller objects. With reference to the observed association between these species of *Plethodon* and large objects, it should be emphasized that areas of the grid without large objects were scrutinized for salamanders just as carefully as were those areas with large objects.

The distribution of the 2 species relative to each other may reflect an interaction between the adults of these 2 closely related species, but a firm conclusion relative to this matter must await further investigation.

Acknowledgment

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